



Forest canopy gaps offer a window into the future: The case of subtropical coastal forests within an urban matrix in South Africa

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Abstract

Aim of study: Alien and indigenous species emergence patterns within canopy gaps in urban subtropical forests are poorly understood. This study compared canopy gap floristics in relation to abiotic and physical characteristics across three subtropical urban forests differing in disturbance history.

Area of study: Three Northern Coastal Forests of varying disturbance histories located in coastal subtropical urban KwaZulu-Natal (KZN), South Africa (SA).

Main results: Closed canopy ($n = 15$ quadrats per forest) and four gaps ($n = 12$ quadrats per forest) from three size classes ('small' < 25 m², 'medium' 25 - 45 m²; 'large' > 45 m²) were surveyed for the primary least disturbed (PLD), primary highly disturbed (PHD) and transitional highly disturbed (THD) forests using classical vegetation sampling techniques. Soil moisture content and air temperature were measured within each gap.

Research highlights: Cumulatively all forest gaps hosted 198 species. Equivalent number of species (Hill numbers from $H = 0$ to $H = 2$) were constantly higher in the PHD forest followed by the PLD forest and lowest in the THD forest. Alien and indigenous plant density were negatively correlated. Species richness was positively correlated with gap size and soil moisture content, and negatively correlated with air temperature.

Keywords: conservation; disturbance; gaps; management; Northern Coastal Forest; subtropical; species richness.

Abbreviations used: conservation; disturbance; gaps; management; Northern Coastal Forest; subtropical; species richness.

Authors' contributions: A.B., S., K.P. and S.R. conceived the idea. A.B. and O.K.K. conducted data collection. AB conducted data analyses. A.B., S.R. and S. led the writing, with contributions from K.P.

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Introduction

As in many parts of the developing world, indigenous forests in South Africa (SA) are experiencing a sustained decline in both spatial cover and diversity, due mainly to increased natural and anthropogenic disturbances (Ahrends *et al.*, 2010; Bhugeloo *et al.*, 2019). Both natural and anthropogenic disturbances shape forest structural and spatial patterns by creating canopy gaps (Runkle, 1981; McCarthy, 2001), defined as breaks in the canopy created by a disturbance event (Murphy *et al.*, 2006) and given their regenerative potential, are considered a key driver of local species diversity and maintenance (Maranho *et al.*, 2016; Massad *et al.*, 2019). Changes in light, air

temperature, soil nutrient availability, evapotranspiration levels and competitive interactions in canopy gaps relative to an intact canopy all influence species composition within gaps, and the subsequent overall forest regeneration and recovery patterns (Yamamoto, 2000; Asner *et al.*, 2013; Lu *et al.*, 2019).

Gap size can influence several biotic and abiotic variables, consequently influencing tree species regeneration (Muscolo *et al.*, 2014; Lu *et al.*, 2018). The size-frequency distribution of forest gaps can therefore provide information on the disturbance and subsequent recovery status and potential of forests (Coates, 2000; Chen *et al.*, 2019). For example, early colonising light dependant species (pioneer species) recruit into larger gaps while later

colonising shade tolerant species (climax species) recruit under the forest canopy or in smaller gaps (Whitmore, 1989; Obiri & Lawes, 2004). Climax species require minimal light to reach maximum growth and development and regenerate until the gap is eventually closed (McCarthy, 2001). These species-specific characteristics give rise to the gap phase cycle of regeneration, which is considered an integral part of the growth cycle of forests, determining the forest's ultimate floristic composition (Whitmore, 1989).

Advanced regeneration involves seedlings and saplings already present within a gap at the time of gap formation and coupled with seedling recruitment that occurs after gap formation, can be referred to as the gap dynamics of a forest (Muscolo *et al.*, 2014). Most species that regenerate within the gaps are due to advanced regeneration as these species quickly outcompete species that emerge from the seed bank (Yamamoto, 2000). Forests gap dynamics is fundamental to the community structure and play a central role in species abundance and turnover in forests flora (Obiri & Lawes, 2004).

Disturbances create the opportunity for species to colonise a gap, including species lying dormant in the seed bank (Grubb *et al.*, 2013). However, under low disturbance conditions, dormant seeds in the seed bank are not given the opportunity to recruit into the gaps. Spatial and temporal variation within gaps (niche partitioning) created by intermediate disturbances can therefore allow climax and pioneer species to co-exist leading to high species diversity (Obiri & Lawes, 2004; Sharma *et al.*, 2018).

Natural and anthropogenic disturbances are also considered to be the main determinants of alien plant invasion, providing corridors that facilitate the dispersal and establishment of alien species (D'Antonio & Meyerson, 2002; Alston & Richardson, 2006). The change in light, temperature, soil nutrients and increase in space that are associated with canopy gaps formation, promote indigenous and alien plant seed germination (D'Antonio & Meyerson, 2002). Generally, alien plant species have large persistent seed banks and are faster growing than indigenous types, allowing alien species to maximise the sudden availability of resources, leading to their dominance in the post-disturbance environment (D'Antonio & Meyerson, 2002; Gioria & Pyšek, 2015). Continual, as opposed to episodic, disturbances lead to fragmentation of indigenous vegetation patches, giving rise to edge effects within urban matrices. This can result in increased abundances of alien species and altered disturbances regimes (Alston & Richardson, 2006). In a forest, edge effects can also occur at the interface of a canopy gap and intact canopy.

Whilst we do have some understanding of how natural disturbances influence gap dynamics in forests (Asner *et al.*, 2013), data on gap dynamics in remnant forest patches within urban settings subject to both natural and anthropogenic disturbances are scarce (Massad *et al.*, 2019).

This South African case study compared gap floristics (species richness, density, Hill numbers and floristic similarity) in relation to abiotic (air temperature, soil moisture, wind speed and relative humidity) and physical (area) characteristics across three patches of Northern Coastal Forest (NCF) (Mucina *et al.*, 2006) with differing disturbance histories. The research questions addressed in the context of NCF in KZN were as follows: (i) How does disturbance affect the floristic composition of the canopy gaps? (ii) What is the relationship between canopy gap size and its floristic composition? (iii) Does disturbance affect floristic similarity between the intact canopy and the canopy gaps? (iv) What is the influence of disturbance on abiotic characteristics of canopy gaps?

Data on canopy gap structure, abiotic characteristics, species composition and vegetation structure are crucial for designing conservation and management strategies such as species reintroduction and alien plant eradication and/or control. Gap centred management strategies are likely to become increasingly important in urban forest patches, given their vulnerability to natural and anthropogenic disturbances (Sharma *et al.*, 2018).

Methods

Study Sites

Three NCF patches in KwaZulu-Natal (KZN, SA), located within the Indian Ocean Coastal Belt (IOCB) biome, were selected for investigation. Northern Coastal Forest is a subtropical forest type that has been under increasing pressure from agriculture, timber plantations, urban development, heavy metal mining and illegal clearing over the last few decades (Mucina *et al.*, 2006). The three forest patches selected for investigation were the uMdoni, Hawaan and uMdloti forests (Fig. 1; Table 1).

uMdoni Forest is a primary forest with high levels of disturbance (primary highly disturbed [PHD]), due to a surrounding golf course and its associated activities. Parts of the forest that have expanded beyond the borders of the golf course are subject to uncontrolled clearing, harvesting and burning, illegal access and informal pathways, making these portions clearly distinguishable from the access-controlled primary forest (Kambaj *et al.*, 2018).

Hawaan Forest is a primary forest with low levels of disturbance (primary least disturbed [PLD]). It has been fully fenced and access controlled for approximately 50 years, with regular clearing of alien vegetation over the last decade. However, small parts (almost exclusively the fringes) of the forest are subject to illegal access, informal pathways, and some clearing and harvesting (Kambaj *et al.*, 2018).

uMdloti Forest is a transitional forest that contains a mosaic of primary and secondary forest with high levels

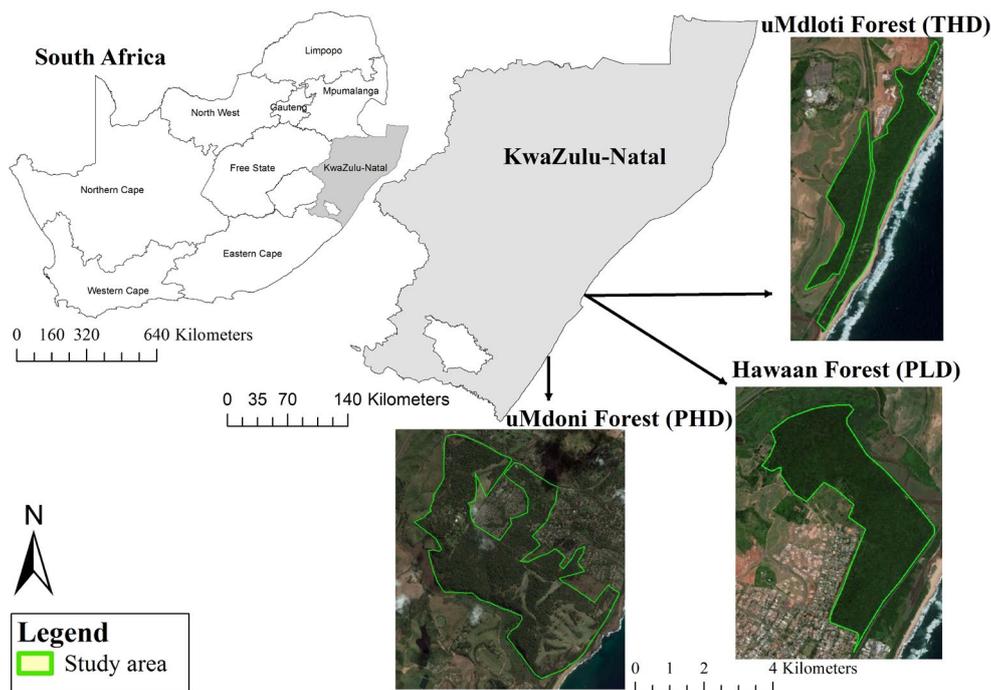


Figure 1. Location of the three forests PLD: primary least disturbed; PHD: primary highly disturbed; THD: transitional highly disturbed) in KwaZulu-Natal, South Africa.

of disturbance (transitional highly disturbed [THD]). A transitional forest is classified as a forest that experiences increasing forest cover following a period of decreased forest cover, due primarily to land use changes (Mather, 1992). Previously, the uMdloti Forest experienced unrestricted access resulting in the creation of footpaths and informal settlements within the forest. A portion of primary forest is now access controlled through fencing (for *c.* 5 years).

Gap selection and characterisation

At each forest twelve gaps of varying size classes ('small' gaps < 25 m², 'medium' gaps between 25 - 45 m²;

'large' gaps > 45 m²) were sampled during the summer season (November–December 2016). Canopy gaps were defined as an opening in the canopy due to complete or partial loss of trees extending to the forest undergrowth (Obiri & Lawes, 2004). The gaps were selected via parallel walked transects (three to five that were > 75 m apart) within the physiognomically mature (primary) parts of the forests. The boundary and centre point of each gap was recorded using a handheld GPS (Garmin Etrex 20x, Garmin, Kansas, United States of America). Gaps were placed into different size classes based on area. Area (A) was calculated following Runkle (1992), as follows: $A = \pi LW/4$, where L = gap length (longest distance between two gap edges) and W = gap width (longest distance perpendicular to length). A total of 15 small gaps, 12 medium

Table 1. Site characteristics of the uMdoni (PHD), Havaan (PLD) and uMdloti (THD) forests

Forest	Size (ha)	Altitude (m above sea level)	Central co-ordinates	Disturbance history
PHD	200	26	30°23'53.23"S 30°41'16.77"E	Historical disturbance but *Protected > 10 years
PLD	55	71	29°42'38.30"S 31°5'24.20"E	**Protected > 50 years
THD	105	37	29°40'49.64"S 31°6'38.73"E	Historical disturbance but protected < 10 year

* Perimeter partially fenced with access controlled primary forest **Perimeter fully fenced and access controlled

gaps and nine large gaps were sampled across the forests, ensuring sufficient variability in gap sizes sampled.

Air temperature, relative humidity and wind speed were measured in all gaps using a 4500 Pocket Weather Tracker (Kestrel, Birmingham, United Kingdom) at midday. Soil moisture content was also measured for each gap using a soil moisture meter (HH2 Moisture Meter, Delta-T Devices, Cambridge, United Kingdom).

Vegetation surveys

Plant species abundance was recorded for each gap ($n = 12$ gaps for each forest) and within the intact canopy ($n = 15 \times 225 \text{ m}^2$ quadrats per forest) in all three forests. Individuals were placed into growth stage (seedling, sapling, shrub, and tree) and life form (graminoid, climber, herb, shrub, and tree) categories. Diameter at breast height (DBH) was measured for each tree present in the gaps. Voucher specimens of each species were deposited at the Ward Herbarium (University of KwaZulu-Natal, Westville Campus, Durban). Specimens were identified to species level. In a few cases, seedlings were very young and could only be identified to genus level. Comprehensive checklists of all plant species identified within the gaps of each forest were compiled. Indigenous species names and authorships follow the South African National Biodiversity Institute's (SANBI) online Plants of southern Africa (New POSA) (SANBI, 2020a). The conservation status of indigenous species was based on SANBI's Red List of South African Plants (SANBI, 2020b). Alien taxa were categorised according to the National Environmental Management: Biodiversity Act (NEMBA) (10 of 2004) (Department of Environmental Affairs [DEA], 2004) and the alien and invasive species list (DEA, 2016). Plants were also classified according to demographic size classes: individuals $< 10 \text{ cm}$ tall were classified as seedlings, individuals $> 10 \text{ cm}$ tall showing no reproductive traits were classified as saplings and individuals showing reproductive traits (*e.g.* production of buds and flowers) were classified as mature individuals.

Data analysis

Species accumulation curves were constructed for gap and intact canopy data (EstimateS 9.0, Colwell, 2013) to determine sampling effort. Sampling effort was calculated using the Jack1 and Chao2 estimators. An 80% sampling effort was achieved for the intact canopy (Kambaj *et al.*, 2018). The finite number of gaps present in each forest did not allow for sampling to continue until an 80% sampling effort was achieved. Consequently, the Jack1 and Chao2 estimators provided only a modelled species estimate for the gap dataset. Graminoids were excluded from

the assessment of sampling effort as abundance data could not be collected due to their clonal habit (Kambaj *et al.*, 2018). Species richness, Shannon's exponential and Simpson's inverse (denoted as 0H, 1H and 2H, respectively in the Hill numbers nomenclature) were also computed (EstimateS 9.0, Colwell, 2013; RStudio, Version 1.2.1335, RStudio Inc., 2019) to compare alpha diversities across forest sites (all taxa, including graminoids). Species richness (all taxa) at each site was compared between intact canopy and canopy gaps using the Jaccard and Sørensen indices, based on presence-absence data (after Sershen *et al.*, 2019).

A one-way analysis of variance (ANOVA) was used to test for significant differences in floristic and abiotic parameters across forests (data were parametric). The relationship between gap area and species richness was assessed using Pearson's correlation analysis. Pearson's correlations (parametric data) or Spearman's rank correlation analysis (non-parametric data) were also used to assess for relationships between selected abiotic (air temperature and soil moisture) and floristic (species richness, abundance and density of indigenous and alien species) parameters. Pearson's correlation analysis (parametric data) was also used to assess the relationship between indigenous seedlings and saplings, alien seedlings and saplings, and between mature indigenous alien plants.

Cluster and ordination analyses were used to assess the similarity among the three forests ($n = 3$) and gaps of different size classes (with data from all three sites pooled; $n = 36$). The presence-absence data were used to generate a similarity matrix based on the Bray-Curtis index and clustering was then performed using the unweighted pair group method with arithmetic mean (UPGMA). A non-metric multi-dimensional scaling (NMDS) ordination was also conducted on square root-transformed species abundance data, in three dimensions, using the Bray-Curtis index for gaps of all three forests combined ($n = 36$). The ordination was evaluated using the 'stress' coefficients (a measure of disagreement between values in ordination space). Stress co-efficients < 0.20 were considered well-represented interpretations (Kruskal 1964; Clarke, 1993). Graminoids were excluded from the NMDS analysis (given the absence of abundance data) but included in the UPGMA cluster analysis. All statistical analyses were performed using RStudio (Version 1.2.1335, RStudio Inc., 2019) and PAST (Version 3.25, Paleontological Statistics, 2019) (Hammer *et al.*, 2001).

Results

Canopy gap floristics

The floristic survey across all three forests canopy gaps collectively identified 198 species belonging to 63

families (Table S1 [suppl.]). The most species rich forest was the primary highly disturbed forest (PHD) with 136 species (56 families). One hundred and fifteen species (44 families) were identified in the primary least disturbed forest (PLD), and 54 species (35 families) in the transitional forest with high levels of disturbance (THD) (Fig. 2). Thirty species and 29 families were shared amongst all three forests.

The three most dominant families when data for all three forests were pooled were Rubiaceae, Fabaceae and Asteraceae with 23, 21 and 18 species, respectively. Rubiaceae (12), Asteraceae (10) and Fabaceae (9) were the most speciose in the PHD forest. At the PLD forest, the top three families in terms of species richness were Fabaceae (8), Euphorbiaceae (7) and Rubiaceae (7), while at the THD forest, Fabaceae (4) and Rubiaceae (4) were the top two families. Several families, viz. Asteraceae, Malvaceae, Poaceae, Rutaceae and Vitaceae, ranked third at the THD forest, each with three species.

One taxa of conservation concern taxa, *Atalaya natalensis* R.A.Dyer (Sapindaceae, listed as 'Near Threatened') (SANBI, 2020b), occurred in the gaps and the PHD forest only. Collectively, 15 alien plant species were identified across the three forests: 11 Invasive Alien Plant Species (IAPs), of which 10 species are classified as Category 1b (invasive species that must be controlled and wherever possible, removed and destroyed; trading and planting is strictly prohibited) and one species is Category 3 (invasive species that are allowed to remain in prescribed areas; trading and planting is prohibited) (DEA, 2016). The remaining four species are classified as naturalised exo-

tic species (SANBI, 2020a). Thirteen alien species were found at the PHD (nine Category 1b IAPs; one Category 3 IAPs; three naturalised exotics), six at the PLD (four Category 1b IAPs and two naturalised exotics), and eight at the THD (six Category 1b IAPs and two naturalised exotics). The THD had the highest (15% of total number of species) level of alien species representation, followed by the PHD (10% of total number of species) and the PLD (5% of total number of species).

Correlation analyses on density data for all forests combined revealed significant negative correlations between indigenous seedlings and saplings and alien seedlings and saplings ($r = -0.999$; $p < 0.05$) and between mature indigenous alien plants ($r = -0.998$; $p < 0.05$).

Canopy gap and intact canopy floristic similarity

Collectively, 217 species belonging to 70 families were found in the intact canopy of all forests, while 198 species belonging to 63 families were found in gaps. Shared species between canopy gaps and intact canopy in PHD included 81 of the 199 total species found (41%). Shared species between canopy gaps and intact canopy in PLD amounted to 76 of the 149 total species found (51%). Shared species between canopy gaps and intact canopy in THD amounted to 53 of the 64 total species found (83%). This together with the results of similarity analyses (Table 2) illustrates that proportion of taxa shared between gap and intact canopy can vary greatly across forests.

The three most abundant species in terms of density in PHD gaps were *Trifolium repens* L. (9.18% of total density), *Kedrostis foetidissima* (Jacq.) Cogn. (6.94% of total density) and *Cyperus albostratus* Schrad. (6.02% of total density) while *Englerophytum natalense* (Sond.) T.D.Penn. (10.93% of total density), *Monanthon caffra* (Sond.) Verdc. (6.70% of total density) and *Drypetes arguta* (Müll.Arg.) Hutch. (5.79% of total density) were the most abundant species in the PHD intact canopy. In PLD gaps, *Asparagus plumosus* Baker. (11.66% of total density), *Hibiscus cannabinus* L. (8.64% of total density) and *Achyranthes aspera* L. (7.95% of total density) were the three most abundant species in gaps while *Cola natalensis* Oliv. (3.90% of total density), *Uvaria caffra* E. Mey. ex Sond. (3.78% of total density) and *Achyranthes aspera* L. (3.65% of total density), were the most abundant in intact canopy within this forest. The most abundant species in THD gaps were *Ageratum houstonianum* Mill. (22.49% of total density), *Laportea peduncularis* (Wedd.) Chew. (13.1% of total density) and *Lantana camara* L. (12.58% of total density) while *Vitellariopsis marginata* (N.E.Br.) Aubrév. (11.89% of total density), *Kedrostis foetidissima* (Jacq.) Cogn. (9.13% of total density) and *Laportea peduncularis* (Wedd.) Chew. (8.69% of total density) were the most abundant species

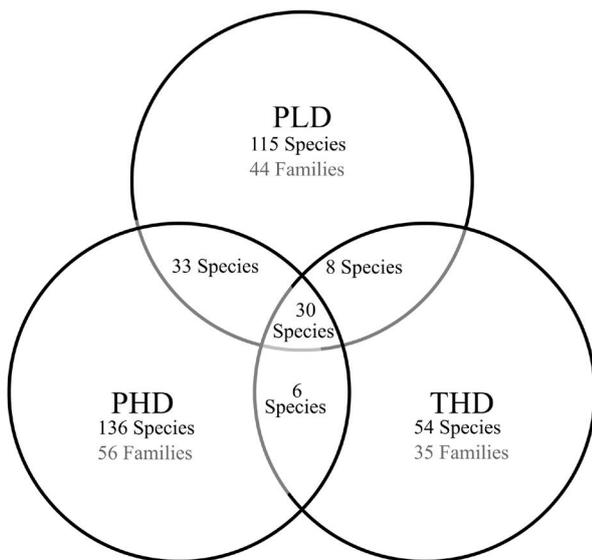


Figure 2. Venn diagram showing number of species (black numbers) and families (grey numbers) found in canopy gaps ($n = 12$ gaps per forest) at the three forests (PLD: primary least disturbed; PHD: primary highly disturbed; THD: transitional highly disturbed), and the number of species shared between forests.

Table 2. Sørensen and Jaccard similarity values for comparisons between canopy gaps and intact canopies within each forest investigated and between canopy gaps of different forests (PLD: primary least disturbed; PHD: primary highly disturbed; THD: transitional highly disturbed).

Forest/Component	Sørensen similarity value			Jaccard similarity value		
	PHD gaps	PLD gaps	THD gaps	PHD gaps	PLD gaps	THD gaps
PHD intact canopy	0.579	-	-	0.407	-	-
PHD gaps	-	0.531	0.402	-	0.362	0.252
PLD intact canopy	-	0.691	-	-	0.527	-
PLD gaps	-	-	0.476	-	-	0.312
THD intact canopy	-	-	0.946	-	-	0.898

in the THD intact canopy. It should be noted here that *L. camara* and *A. houstonianum* are both Category 1b IAPs. The lack of common taxa in gaps and closed canopy confirms the stochastic nature of species recruitment often expected in gaps (Obiri & Lawes, 2004).

Shannon's exponential index (1H) provides an indication of the equivalent number of commonly occurring species while the Simpson's inverse index (2H) reflects the equivalent number of abundant species found at a site (Chao *et al.*, 2014). Finally, Chao2 index provides an indication of the maximum number of species that could be found at a site with the maximum sampling effort. Hill numbers have not been used in species assemblages studies until recently (particularly in forest gap studies). The PHD forest gaps displayed the highest number of possible species (Chao2 index = 188.15) as well as the highest number of species, commonly occurring species and abundant species ($0H = 136$; $1H = 51.71$ and $2H = 30.34$). PLD forest gaps reached intermediate values for the number of possible species (Chao2 index = 140.01) as well as the number of species, commonly occurring species and abundant species ($0H = 115.6$; $1H = 42.85$ and $2H = 23.18$). The THD forest gaps displayed lowest values for the number of possible species (Chao2 index = 93.71) and the number of species, commonly occurring species and abundant species ($0H = 59$; $1H = 17.53$ and $2H = 10.31$). Calculation of these indices offers a congruent comparative of the plant diversity status in the gaps of the three forest sampled (Fig. 3).

Hill numbers and the Chao 2 index were also calculated for gap size classes, by pooling the canopy gap data for the three forests (Fig. 4). As expected, calculations revealed that size class 3 ('large' gaps > 45 m²) displayed the highest number of possible species (Chao2 index = 194.73) and highest Hill numbers ($0H=140$, $1H = 114.82$ and $2H = 94.34$). The size class 2 ('medium' gaps between 25 - 45 m²) values were intermediate for the Chao2 index (= 166.38) and Hill numbers ($0H=127$; $1H = 95.67$ and $2H = 76.97$), and size class 1 ('small'

gaps < 25 m²) displayed the lowest values for the Chao2 index (= 148.02) and Hill numbers ($0H=122$; $1H=92.35$ and $2H = 73.47$).

Sørensen and Jaccard similarity indices were used to compare the canopy gaps across the three forests. Both indices indicate differing levels of similarity in terms of species richness between intact canopy and canopy gaps across the three forests. In general, the gap and canopy similarity for each forest was highest when compared to the gaps and canopies of the other two forest. The THD forest showed the highest levels of similarity between intact canopy and canopy gaps while the PLD and PHD forests showed markedly lower similarities between intact canopy and canopy gaps (for both indices). The PHD and PLD forest gaps displayed the highest levels of similarity to each other in terms of species richness, while the highest levels of dissimilarity were between the PHD and THD forest gaps (Table 2).

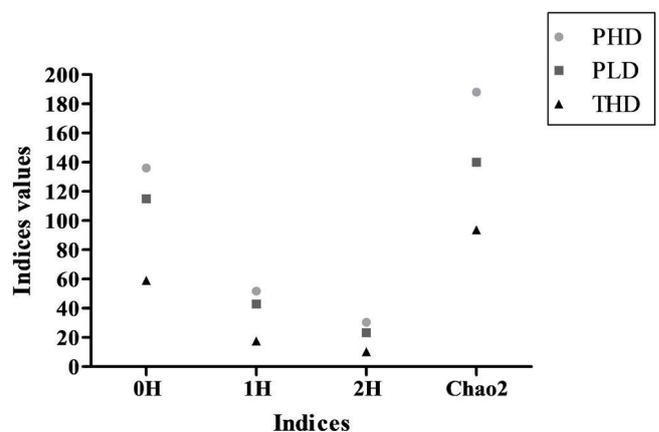


Figure 3. Equivalent number of species by Hill numbers ($0H$ = species richness; $1H$ = Shannon's exponential; $2H$ = Simpson's inverse) and predicted species using the Chao2 index, for canopy gaps in the primary highly disturbed (PHD), primary least disturbed (PLD), and transitional highly disturbed (THD) forests investigated.

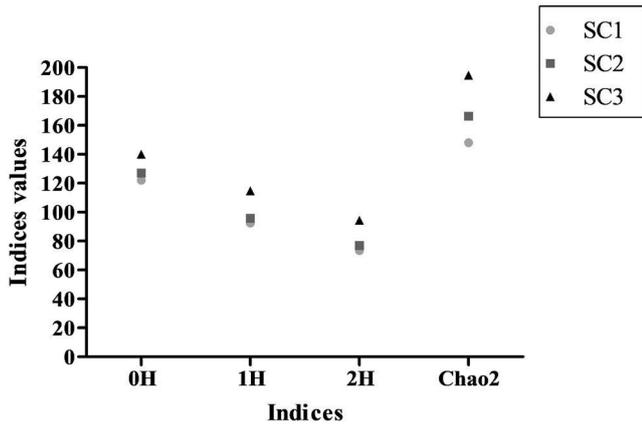


Figure 4. Equivalent number of species by Hill numbers ($0H$ = species richness; $1H$ = Shannon's exponential; $2H$ = Simpson's inverse) and predicted species using the Chao2 index, for canopy gap size classes (SC) based on pooled data from the three forests investigated (SC 1: gaps < 25 m²; SC 2: gaps between 25 - 45 m²; SC 3: gaps > 45 m²).

Relationship between species richness and canopy gap area

Pearson's correlation analyses were used to assess the relationship between species richness and gap size class for each forest. There was a trend for species richness to be higher in larger gaps in the PLD forest; however in a

few cases across all three forests, smaller gaps had greater species richness than larger gaps (Fig. 5a). There was a significant positive relationship between species richness and gap area for the PHD forest (Fig. 5b). No clear relationship between species richness and gap area was observed for the THD forest (Fig. 5c). A significant positive correlation between species richness and canopy gap area when data for all three forests were pooled for analysis, was also revealed, *i.e.* species richness was higher in larger gaps (Fig. 5d).

Floristic similarity of canopy gaps

The UPGMA cluster analysis was used to determine floristic similarity of canopy gaps among forests, and was based on presence/absence data for the 198 species (including graminoids) found in all gaps across the three forests. There are three main clusters (THD, PHD and PLD) at approximately 0.27 similarity (Fig. 6). The clusters are forest-specific and appear to reflect the differences in disturbance history across the three forests: the highly disturbed forests (THD and PHD) grouped together, indicating that these forests are more similar to each other than to the PLD forest. It is also worth noting that gaps of the same size class did not always group within a forest, *i.e.* gap size did not influence floristic similarity (not shown). The NMDS analysis also recovered the same results (Fig. S1 [suppl.]).

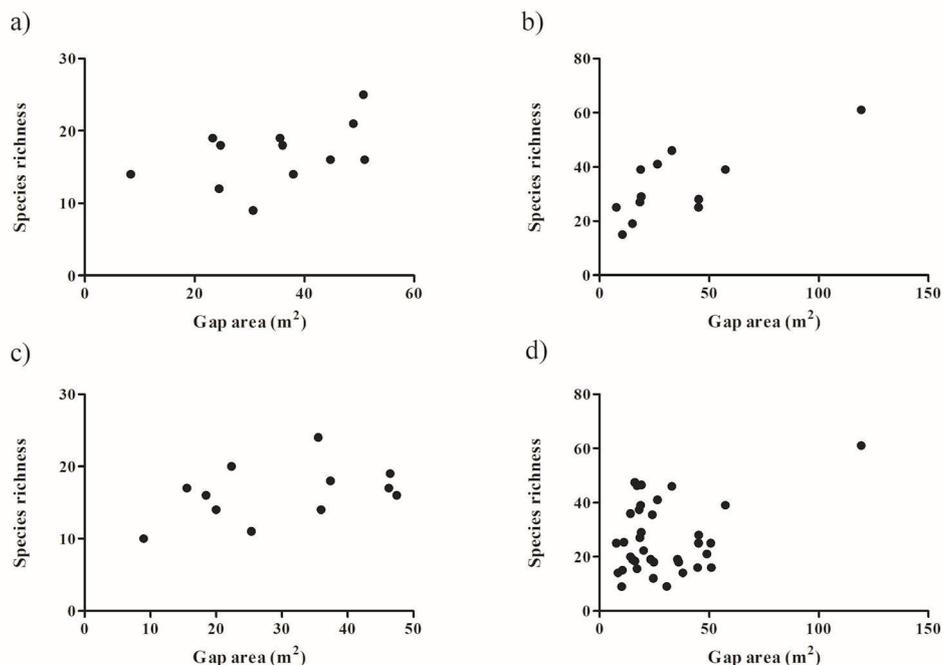


Figure 5. Correlation analyses for species richness versus canopy area for the, a) Primary least disturbed ($n = 12$; $r = 0.461$; $p > 0.05$), b) Primary highly disturbed ($n = 12$; $r = 0.752$; $p < 0.05$) and c) Transitional highly disturbed forests investigated ($n = 12$; $r = 0.423$; $p > 0.05$); d) data for all forests pooled ($n = 36$; $r = 0.521$; $p < 0.05$).

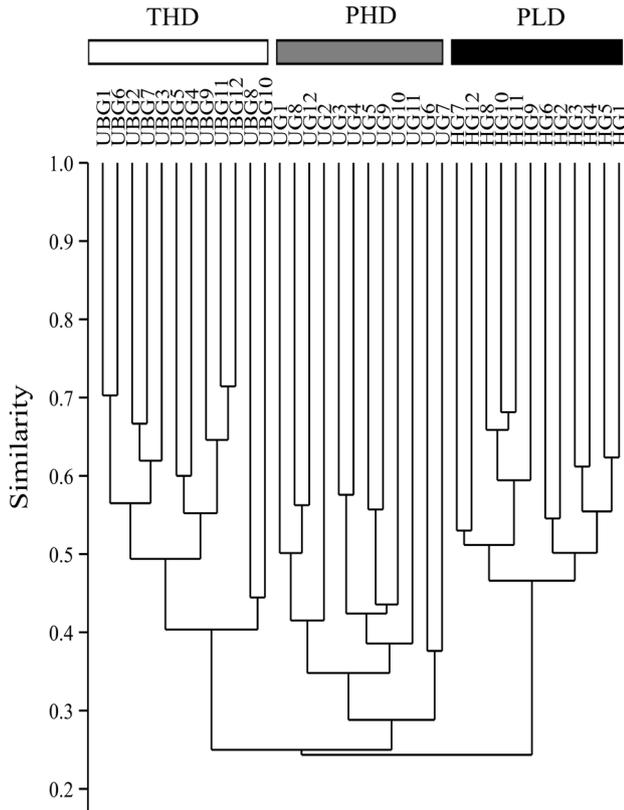


Figure 6. Unweighted pair group method with arithmetic mean (UPGMA) phenogram for the THD (transitional highly disturbed) ($n = 12$ gaps), PHD (primary highly disturbed) ($n = 12$ gaps) and PLD (primary least disturbed) ($n = 12$ gaps) forests. Bars denote the forest specific clusters.

Relationship between floristic and abiotic factors in canopy gaps

When canopy gap data for all forests were pooled there was a significantly negative correlation between species richness and canopy gap air temperature ($r = -0.582$; $p < 0.05$), as well as between canopy gap plant density and air temperature ($r = -0.505$; $p < 0.05$). Species richness was significantly positively correlated with soil moisture content ($r = 0.424$; $p < 0.05$). When these relationships were tested within each forest, there was a strong positive correlation between species richness and soil moisture content for the PHD forest only ($r = 0.676$; $p < 0.05$).

Discussion

How does disturbance affect the floristic composition of canopy gaps?

Although natural and anthropogenic disturbances are considered key drivers of biodiversity and species richness in subtropical forests, anthropogenic pressures have increased the rate of disturbance events, leading to

a decline in forest cover and species richness over time (McCarthy, 2001). Although the three forests differed in disturbance history and intensity, Rubiaceae, Fabaceae and Asteraceae were the most dominant families within canopy gaps. These families are common Angiosperm families that have a high number of species globally (Angiosperm Phylogeny Website [APW], 2019), are well represented in South African flora and their representatives are characteristic of NCF patches across KZN (Kambaj *et al.*, 2018). For example, Kambaj *et al.* (2018) showed these three families to be among the most speciose in the intact canopy of three remnant patches of NCF that differed in levels of non-natural disturbance and protection.

The THD forest gaps displayed the lowest species richness which was also reflected in intact canopy vegetation. The similarity in the values of 1H and 2H for this forest indicate that many of the species that are common are in turn abundant, suggesting a dominance in competition with other possible colonizing species. In younger forests such as the THD forest, high disturbance levels can lead to lower species richness and higher evenness as the more competitive species are likely to dominate cleared sites (Huston, 2004). The seed bank of the THD forest may have also been species poor compared with the primary forests, making a minimal contribution to species richness in the standing vegetation.

In relatively stable environments where disturbance is minimal, interspecific competition is expected to be lower than in more disturbed environments due to fewer opportunities for new species to emerge and establish in stable environments, leading to intermediate species richness, number of commonly occurring species and equivalent number of abundant species as displayed by the PLD forest (Feldmann *et al.*, 2018). New species are given opportunities to establish themselves in disturbed systems but experience higher competition levels and greater instability, leading to increased species richness and lower evenness across a site, as seen in the PHD forest (Huston, 2004). Similarly, in the gaps of the PLD forest easily dispersed, quick to establish graminoids (*e.g. Oplismenus hirtellus* (L.) P.Beauv. and *Ehrharta calycina* Sm.), occurred at high densities (Wittkuhn, 2010; Hawkins & Suss, 2011). These early gap fillers may have inhibited woody species from recruiting in the gaps within the PLD forest, contributing to lower species richness than the PHD forest (Sharma *et al.*, 2016).

The three forests were not of a comparable age so the intermediate disturbance hypothesis (IDH) cannot be used to explain the differences in species richness and evenness observed in this study. Nevertheless, disturbance, such as the creation of canopy gaps, helps increase species richness by providing environmental heterogeneity for multiple light and shade dependent species to co-exist, increasing overall species richness in highly disturbed areas (Gravel *et al.*, 2010; Vargas *et al.*, 2010; Lu *et al.*, 2019). Alien species

are also generally more abundant in highly disturbed environments (PHD and THD forests) as they tend to be prolific in reproductive strategies, seed for longer and at high levels, have larger more persistent seed banks and efficiently exploit the availability of resources to help ensure their dominance over indigenous species (Gioria & Pyšek, 2015).

In terms of density, however, the PLD forest gaps had the highest density of indigenous species in each gap. Overall, results from this study suggest that species richness and the number of typical and abundant species within gaps may be the product of disturbance, age of the forest patch, stage of gap infilling and possibly the seed bank profile.

Despite the differences in species richness across forests, the three forests shared a number of species ($n = 30$; 26 indigenous species), indicating that certain elements of the NCF floristic signature persist even at high levels of disturbance (e.g. *Brachylaena discolor* DC., *Euclea natalensis* A.DC. and *Strelitzia nicolai* Regel & Körn.). Similarly, intact canopy vegetation in the three forests also shared a high number of species across forests ($n = 151$), supporting previous reports of the persistence of the NCF signature in disturbed forest patches (Kambaj *et al.*, 2018). The two primary forests (PLD and PHD) shared the most species ($n = 63$) in terms gap vegetation, despite the differences in disturbance history. Transitional forest patches can be very different from primary forest patches in terms of species composition (Mather, 1992), as was the case in this study. The PHD forest exhibited the highest number of unique species, possibly attributed to the large size compared to the other forests (200 hectares) and high overall species richness of the forest.

Only one species of conservation concern (*Atalaya natalensis* R.A.Dyer) occurred in the PHD gaps, despite several species of conservation concern occurring in the PHD intact canopy. *Atalaya natalensis* is considered a rare fruit bearing forest tree that occurs in KZN (Boon, 2010). No species of conservation concern occurred in the PLD or THD gaps, despite several species of conservation concern occurring within the PLD intact canopy.

Importantly, two alien invasive species, viz. *Lantana camara* and *Ageratum houstonianum*, were among the most abundant species at the THD forest in both intact canopy and canopy gaps. Both species are classified as Category 1b IAPs and are commonly found in KZN coastal forests (DEA, 2016). In the THD forest, alien and indigenous plants also occurred at comparable densities within gaps, despite recent management efforts. It is advised that more intense alien plant removal efforts be implemented at this forest. However, the removal of alien species can also constitute a disturbance event, since the soil surface is disturbed and a clearing is created which could allow opportunistic alien species within the seed bank to germinate (D'Antonio & Meyerson, 2002; Gioria & Pyšek, 2015), resulting in secondary invasions. Management efforts that include the removal of alien species should therefore be accompanied

by an indigenous revegetation plan to prevent alien (and/or weedy) species that often lie dormant in the seed bank from re-emerging and establishing (D'Antonio & Meyerson, 2002; Massad *et al.*, 2019).

The promotive effects of disturbance on alien abundance in forest systems are generally considered to have negative impacts on indigenous species (D'Antonio & Meyerson, 2002). In this study, alien species were present as seedlings, saplings and mature individuals in all three forests and their presence appears to be having a negative effect on indigenous species in terms of density. However, intact canopy had lower levels of alien prevalence than gaps in terms of cover and abundance in all three forests, suggesting that alien plants may be transient gap occupiers. Given that gaps were not revisited over time in this study, it is unclear whether the early emergence of alien species within gaps (Brothers & Spingarn, 1992) could be creating favourable microhabitats in which certain indigenous species could arise in the forests investigated here. However, suggestions of this facilitatory role of certain alien taxa in other studies (D'Antonio & Meyerson, 2002; Rodriguez, 2006) warrants further investigation of this possible phenomenon in NCF gaps.

The UPGMA and NMDS analyses based on gap flora revealed disturbance-specific clusters with the two highly disturbed forests (PHD and THD) grouping closer together than either was to the PLD forest. The potential for disturbance to alter the number and type of species involved in gap infilling within NCF patches is exemplified by the fact that the PLD and the THD forests are in closest proximity to each other (being separated by only the Mhlanga River), yet are highly dissimilar in terms of gap floristic composition.

Does disturbance affect the floristic similarity between the intact canopy and the canopy gaps?

When the floristic similarity between intact canopy and canopy gaps was assessed, species composition in gaps and intact canopy was found to be most dissimilar in the PHD forest and most similar in the THD forest, while the PLD forest showed intermediate levels of similarity. The lowest similarity levels between the PHD intact canopy and canopy gaps, could be due to its high instability. As the forest is continually disturbed, microclimatic conditions are expected to vary substantially across the forest, possibly allowing atypical NCF species to colonise the forest (Obiri & Lawes, 2004). It is also likely that the primary seed bank in the PHD forest is unable to recover due to high levels of sustained/prolonged disturbance (Matlack & Good, 1990). Dispersal and recruitment limitations are negatively affected by high disturbance resulting in many species that rely on dispersal for establishment being unable to colonise gaps shortly after their

creation, leading to low similarity values between gaps and intact canopy (Sharma *et al.*, 2016). The intermediate level of similarity observed between the intact canopy and canopy gaps (considered to be between the highest and lowest similarity values) in the PLD forest is possibly reflective of an intact seed bank and is in agreement with reports for forest systems subject to low levels of disturbance in many parts of the world (Nagel *et al.*, 2010; Devagiri *et al.*, 2016; Feldmann *et al.*, 2018). High levels of evenness and low species richness in the THD forest (*i.e.* canopy gaps and intact canopy combined) may have contributed to the high levels of similarity between gaps and intact canopy including possible advanced regeneration (Abe *et al.*, 1995). The similarity levels between canopy gaps and intact canopy across all forests also indicate that gap infilling is more likely to occur from its intact canopy species pool, rather than from distant canopies of other forests.

What is the relationship between canopy gap size and its floristic composition?

In all three forests, larger gaps generally exhibited higher species richness than smaller gaps, supporting the area-species relationship (Connor & McCoy, 1979). This suggests that the scale and timing of disturbances in terms of gap formation may directly affect gap infilling species richness and evenness in NCF. While it may take a longer time for gap infilling in larger gaps to reach completion, due to the greater forest floor area that will need to be covered, they are likely to host more species than smaller gaps when closed as they potentially have a higher number of microsites available for colonisation (Brokaw & Busing, 2000; Lu *et al.*, 2019). Several studies have also reported a positive correlation between species richness and gap area (Gray *et al.*, 2002; Hill & Curran, 2003; Grainger & van Aarde, 2013; Karki & Hallgren, 2015). However, it should be noted that there were a few small gaps that exhibited relatively high species richness in the present study that could be explained by differences in gap age (*i.e.* some small gaps are possibly older than some of the large younger gaps), the stochasticity of *in situ* seed bank, dispersal dynamics, the rate of gap infilling (*i.e.* older gaps are expected to have higher rates of gap infilling and higher species richness), and regeneration density (Brokaw, 1985; Lu *et al.*, 2018).

What is the influence of disturbance on abiotic characteristics of canopy gaps?

Since the forest floor within canopy gaps are exposed to higher light levels than beneath intact canopy, air temperature within gaps are expected to be higher and soil

moisture levels lower (Gray *et al.*, 2002), as seen for all three forests in this study. As a result of higher light availability in canopy gaps, ground surface temperatures are also expected to be higher than that of intact canopy (Everham *et al.*, 1996; Clinton, 2003).

High temperatures and low soil moisture contents are limiting factors to plant growth in tropical and subtropical forests (Jiang *et al.*, 2016). The significant negative correlation between gap species richness and air temperature, and canopy gap plant density and air temperature (data for all forests combined) is therefore in agreement with the literature. Warmer conditions, as predicted for the KZN region in recent climate change studies (Solecki *et al.*, 2018), could therefore have a negative effect on gap infilling rates and species richness as shown by the significant negative correlation between gap species richness and air temperature, and canopy gap plant density and air temperature (data for all forests combined).

Concluding remarks and recommendations

The comparison of three Northern Coastal Forests differing in disturbance history suggests that levels of unnatural disturbance and management strategies influence floristics within canopy gaps, highlighting the delicate balance of microclimatic conditions required for gap infilling. Canopy gaps in urban forests should be monitored in terms of both size and prevailing abiotic conditions since these factors can influence gap infilling in terms of species compositional pool and rate. Disturbance regimes and forest successional status determine gap floristic patterns and monitoring these patterns can help inform urban forest management strategies such as species reintroduction, alien clearing and enrichment planting within gaps, specifically in disturbed urban forests.

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